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Smallegange, I.M.; van der Meer, J.; Sabelis, M.W.

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Testing a stochastic version of the Beddington–DeAngelis functional response in foraging shore crabs

Isabel M. Smallegange · Jaap van der Meer

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Abstract Current behaviour-based interference models assume that the predator population is infinitely large and that interference is weak. While the realism of the first assumption is questionable, the second assumption conflicts with the purpose of interference models. Here, we tested a recently developed stochastic version of the Beddington–DeAngelis functional response—which applies to a finite predator population without assuming weak interference—against experimental data of shore crabs (*Carcinus maenas*) foraging on mussels (*Mytilus edulis*). We present an approximate maximum likelihood procedure for parameter estimation when only one focal individual is observed, and introduce 'correction factors' that capture the average behaviour of the competing but unobserved individuals. We used the method to estimate shore crab handling time, interaction time, and searching rates for prey and competitor. Especially the searching rates were sensitive to variation in prey and competitor density. Incorporating constant parameter values in the model and comparing observed and predicted feeding rates revealed that the predictive power of the model is high. Our stochastic version of the Beddington–DeAngelis model better reflects reality than current interference models and is also amenable for modelling effects of interference on predator distributions.

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I. M. Smallegange · J. van der Meer
Department of Marine Ecology and Evolution,
Royal Netherlands Institute for Sea Research (NIOZ),
Den Burg, The Netherlands

Present Address:
I. M. Smallegange (✉)
Division of Biology, Imperial College London,
Silwood Park, Ascot SL5 7PY, UK
e-mail: i.smallegange@imperial.ac.uk

J. van der Meer
Institute of Ecological Science, Free University,
De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

Introduction

Interference competition is defined as a (reversible) decline in the feeding rate of an animal, caused by agonistic interactions with its competitors (Goss-Custard 1980; Begon et al. 1990, p. 198). Interference between motile animals arises when predators lose prey items to kleptoparasitic competitors (Brockmann and Barnard 1979), or lose valuable foraging time and energy associated in aggressive interactions. Interference can have a significant impact on the distribution of animals across habitats that differ in food quality (Fretwell and Lucas 1970; Parker and Sutherland 1986; Sutherland and Parker 1985). Animals favour habitats of high resource quality, but as more animals aggregate in preferred habitats, the strength of interference increases. At some point, interference may become so intense that animals do better by foraging in habitats of poorer quality, as this is where they experience less interference (Donazar et al. 1999; Sih 1980). If displaced to habitats of insufficient quality, interference competition might even jeopardize survival (Goss-Custard and Sutherland 1997; Sutherland and Dolman 1994). Since interference affects the distribution of animals in a decisive way, there have been many empirical studies to measure the strength of interference (Dolman 1995; Smallegange et al. 2006; Vahl et al. 2005).

Interference models describing how the presence of competitors affects the feeding rate of animals have been used to examine the effects of interference on the patch and habitat choices and on population dynamics of animals

(Holmgren 1995; Norris and Johnstone 1998; Ruxton et al. 1992; Stillman et al. 1997, 2002). Two approaches, one phenomenological and the other mechanistic, have been taken to model interference (Van der Meer and Ens 1997). The phenomenological approach describes how intake rate changes as competitor density increases by means of an empirical relationship. Alternatively, the mechanistic approach extends the basic idea underlying Holling's disc equation [which is that predators are either in a searching state or in a handling state (Holling 1959)] by including a third behavioural state, namely interfering. The transition rates between the behavioural states searching, handling, and interfering comprise the behavioural rules and mechanisms of the foraging process. For example, a transition from handling back to searching implies that a prey item is consumed, and a transition from interfering back to searching implies the end of a fight between two individuals. Since, in contrast to phenomenological models, the behavioural rules of predators are clearly defined in mechanistic models, they provide an excellent way to explore the behavioural basis of interference. For example, a model of interference parameterized for oystercatchers (*Haematopus ostralegus*) and black-tailed godwits (*Limosa limosa*) showed that strength of interference was most sensitive to attack distance, followed by the searching speed of predators (Stillman et al. 1997, 2002).

The basis of current mechanistic models of interference is formed by the Beddington–DeAngelis functional response model. This model was constructed independently by DeAngelis et al. (1975) and Beddington (1975) who respectively used a phenomenological and mechanistic approach to arrive at the same function. Ruxton et al. (1992) built upon Beddington's mechanistic approach to show how specific behavioural rules of the predators reveal the transition rates between different behavioural states. These transition rates between behavioural states are captured in ordinary differential equations (ODEs). From the steady-state solution of the ODEs, Ruxton et al. (1992) arrived at the so-called generalized functional response (Van der Meer and Ens 1997), which gives the intake rate as a function of both prey density and predator density. However, because the steady-state solution they obtained was "messy and uninstructive", a weak interference assumption was made to arrive at a more transparent steady-state solution, which was of greater mathematical convenience to study effects of interference on population dynamics (Ruxton et al. 1992). However, this implies that, despite the fact that these mechanistic models were designed to study interference, they assume that interference—i.e. time spent in aggressive interactions—is sufficiently small (Moody and Houston 1995; Ruxton et al. 1992; Ruxton and Moody 1997). Hence, an inconsistency has been created where workers study interference using a model that assumes weak interference. A second drawback of current mechanistic models of the generalized functional response is that they are deterministic (Holmgren 1995; Moody and Houston 1995; Ruxton et al. 1992; Ruxton and Moody 1997; Smallegange and Van der Meer 2009; but see Yates and Broom 2007 for a stochastic, mechanistic model of kleptoparasitism), implying that the number of competitors is large enough to be treated as a continuous variable (Érdi and Tóth 1988). However, in behavioural studies, the number of competing predators tends to be small. Thus, if results of such studies are used to link mechanistic models of interference to reality, this creates the problem that the theory is based on infinitely large populations, yet the behavioural data encompass that of only a few individuals, observed in a limited number of replicate trials.

Recently, a stochastic version of the Beddington–DeAngelis functional response model has been presented that is valid for a finite number of interfering predators (Van der Meer and Smallegange 2009). This model is based on the theory of stochastic processes and captures the foraging process within a small predator population by means of continuous time Markov chains. This is the simplest way to describe behaviour that is stochastic with respect to duration as well as alternation, and is thus in principle more suited to describe the behaviour of a small number of competitors. It also avoids the inconsistency mentioned previously. If such a model gives an adequate description, it is possible to specify the contributions of different individuals to their agonistic behaviour (interference), and foraging behaviour can be represented by a relatively small set of parameters. In this paper, we present the first application of the stochastic version of the Beddington–DeAngelis model and test its predictions against experimental data to assess its adequacy in describing foraging behaviour and interference. In the first step, we parameterize the model and use behavioural observations on shore crabs (*Carcinus maenas* [L.]) that forage on mussels (*Mytilus edulis* [L.]) to estimate the model's parameters: the time an individual requires to handle a prey item, the duration of an agonistic encounter between two predators, a predator's searching efficiency for prey, and the rate with which a predator encounters conspecifics and engages in agonistic interactions, i.e. its rate of predator discovery. The estimation procedure assumes that the behaviour of all predators in the experiment is observed (Van der Meer and Smallegange 2009). Here, however, we firstly adjust the estimation procedure to the situation where only behavioural data on one focal predator are available and not on its competitors. In the new estimation procedure, which builds upon the one we used in the original model (Van der Meer and Smallegange 2009), we introduce so-called correction factors that capture the average behaviour of the competing individuals. This new procedure should prove useful to a wide range of

biologists, especially field biologists, who generally only have observational data on single individuals. In the second step, we use a model selection procedure to assess if (focal) crabs vary each of these four parameters with changes in the density of conspecifics and availability of prey. In the third step, we assess how well the model describes foraging behaviour by incorporating all parameter estimates in the model to compare the predicted strength of interference with that observed in shore crabs.

Confronting the model to data: methods of parameter estimation

Behavioural observations

The behavioural observations are from two experiments on the foraging behaviour of shore crabs (Smallegange et al. 2006). The experiments were set-up to assess the strength of interference competition in adult male shore crabs that foraged on mussels. The competitive ability of shore crabs is strongly correlated with crab size (Sneddon et al. 1997), and in the experiments, crabs were matched for size as well as other morphological characters (handedness, gender, colour). Prey items were also standardized: mussels were of similar size and fouling organisms attached to the mussels were removed. During the experiments, any consumed mussels were quickly replenished so that prey densities were kept at an almost constant level (Smallegange et al. 2006). Experiments were carried out during daylight hours and under constant laboratory conditions.

The behavioural observations obtained during the experiments encompass the behaviour of a focal crab in terms of (1) the total searching time y_1 (i.e. the total time that a focal crab searches), (2) the total handling time y_2 (i.e. the total time needed to open and consume mussels), and (3) the interference time, for reasons that will become clear below, indicated as $y_3 + y_4$ (the total time that the focal crab spends interfering while searching for and handling mussels). In each trial of the first experiment, the time budget was scored from the moment a focal crab had finished consuming a mussel until it had finished consuming a second mussel. In the second experiment, this period was extended until the focal crab had finished consuming a third mussel. This implies that the number of transitions from searching to handling, n_{12}, equalled 1 in the first experiment and 2 in the second experiment. Likewise, the number of transitions from handling to searching, n_{21}, equalled 1 in the first and 2 in the second experiment. Furthermore, the total number of transitions from either handling or searching to interference, n_{13} and n_{24}, was scored, as was the total number of transitions from interference back to handling or searching, n_{31} and n_{42}.

In the experiments, focal crabs foraged either alone, with one or with three competitors in a tank (foraging area = ¼ m^2). Regretfully, we did not observe two crabs foraging simultaneously and hence we cannot assess the 'zigzag' functional response pattern, which occurs when interference is strong (Van der Meer and Smallegange 2009). In the first experiment 4, 8, 16, and 32 mussels were offered. In the second experiment, the range of mussel densities was increased and 8, 32, and 128 mussels were offered. Crab and mussel densities are expressed as number per ¼ m^2. To estimate the strength of interference competition, we used results obtained at all prey densities, but only for predator densities 2 and 4. We excluded experimental trials with one predator from the estimation procedure because in that case the rate of predator discovery and time spent interfering cannot be estimated. Treatment combinations in the first experiment were replicated five times and eight times in the second experiment. In both experiments, prey density was kept at an almost constant level because the (generalized) functional response describes predation occurring at a constant prey density. Furthermore, because Holling's disc equation and derivatives thereof assume that foraging predators are time-limited rather than digestion-limited, the experiments lasted sufficiently short so that crabs could not reach a digestive limit.

Parameter estimation when only the focal predator is observed

In order to estimate parameters when only the focal predator is observed, focal-predator Markov chains were developed that describe the foraging behaviour of a focal predator in the presence of null, one, two or three predators of equal competitive ability. As in the stochastic version of the Beddington–DeAngelis model (Van der Meer and Smallegange 2009), the foraging process is modelled by means of continuous-time Markov chains. The interference rules are: searching individuals interact with other searchers and with handling individuals, but handling individuals do not interact with other handling individuals. A predator can thus be in one of four behavioural states: searching, *S*, handling, *H*, fighting after searching, *F*, and fighting after handling, *G*.

The states of the Markov chains of the stochastic version of the Beddington–DeAngelis model form the basis for the focal-predator Markov chains. The Markov chains (of the Beddington–DeAngelis model) give all possible combinations of behaviours that the different predators may display at one time. Here, however, we rearrange these chains to form focal-predator Markov chains that only encompass the transitions between those states where the focal crab changes its behaviour. These states are grouped by the four behaviours (*S*, *H*, *F*, *G*) that the focal predator may display ("Appendix: point 1"). A transition between states entails

that the focal individual changes its behaviour from searching to handling or vice versa, or that the focal and another individual start or stop fighting. The transition rate from, for example, the state *S* (the focal predator is searching) to *H* (the focal predator is handling) is the prey capture rate and equals vD, where *D* is the prey density and *v* the rate of searching for prey. Similarly, the transition rate from *SS* (the focal and the other predator are searching) to *HS* (the focal is handling, the other is still searching) equals vD (Fig. 1). From *SSS* to *HSS*, the transition also equals vD, and so on. The transition rate from *H* to *S* is the handling rate and equals λ, and the expected handling time of a prey item is thus $1/\lambda$. The transition rate from *HS* to *SS*, from *HH* to *SH*, and from *SSS* to *HSS* also equal λ. The transition rate from a state with the focal predator searching and one or more other searchers to a state where the focal and another searcher have started a fight is proportional to the number of ways a pair of individuals, of which one is the focal, can be chosen from the population of searchers. Hence in case of the focal searcher and one other searcher, the transition rate equals μ, where μ is the searching rate for predators (Fig. 1). For the focal searcher and two other searching predators, it is 2μ, and for three other searching predators it is 3μ, etc. The transition rate of going from, for example, state *FF* back to *SS* is φ (Fig. 1), which is the transition rate at which fights come to an end. The expected duration of a fight is therefore $1/\varphi$. The transition rates for fights between a

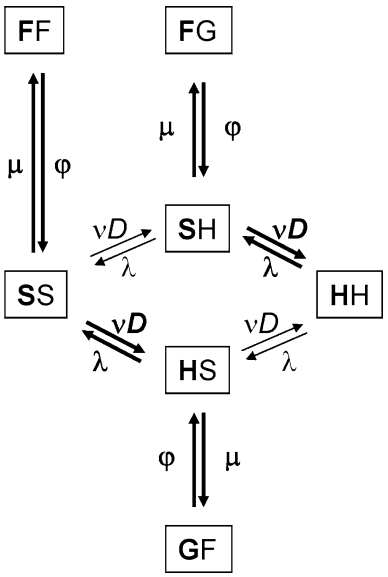

Fig. 1 The 2-predator Markov chain as an example to show the behaviour of the focal predator (in *bold*) and that of the non-focal predator (*non-bold letters*). The states denote searching (*S*), handling (*H*), fighting after searching (*F*), and fighting after handling (*G*), *v* is the searching efficiency, *D* the density of prey, μ the rate of predator discovery, λ the handling time and φ the duration of an interaction. Transitions where the state of the focal predator changes are denoted in *bold*

searching and a handling predator can be derived in the same way (see further the "Appendix: points 1 and 2").

In order to estimate the parameters of a Markov chain that describes behaviour of a focal predator that is dependent on the behaviour of others, the foraging process observed in an empirical study should encompass the behaviour of all predators in the experimental arena. Maximum likelihood estimates of the transition rates can then be obtained from the number of transitions between the states of the Markov chain and the duration that the foraging process is in each state from which the foraging parameters can be calculated (Billingsley 1961; Metz et al. 1983; Haccou et al. 1983; Van der Meer and Smallegange 2009). However, as outlined before, in this study the behavioural observations only encompass the foraging behaviour of one focal individual, and exclude that of the competitors in the arena. This hampers obtaining maximum likelihood estimates of the transitions from *S* to *F* and from *H* to *G* (which depend upon the states of the others), and implies that we cannot resort to the method of maximum likelihood estimation. Nonetheless, estimation of the parameters v, μ, λ, and φ is possible. We have used the assumption that the states of the other predators are at equilibrium. This assumption is asymptotically true as the numbers of predators goes to infinity, once the Markov chain has run for long enough. Whether it also provides a good enough approximation when the actual number of predators is small will be tested by a simulation study (see "Testing the equilibrium assumption").

Generally, the likelihood of the transitions rates q_{ij} in a continuous time Markov chain can be written as $\prod_i \prod_{j\neq i} q_{ij}^{n_{ij}} \exp(-y_i q_{ij})$, where the product is over all possible transitions, n_{ij} is the number of transitions from i to j and y_i is the total time spent in state i (Norris 1997, pp. 87–97). The maximum likelihood estimates of q_{ij} can be obtained by setting the partial derivatives of the log-likelihood $\sum_i \sum_{j\neq i} n_{ij} \log q_{ij} - y_i q_{ij}$ with respect to the q's equal to zero, which gives $\hat{q}_{ij} = n_{ij}/y_i$. An approximate standard error of this estimate is given by the square root of the inverse negative second derivative of the log-likelihood, which equals $\hat{q}_{ij}/\sqrt{n_{ij}}$. This estimation procedure can be approximated for focal-predator Markov chains with states 1–4: *S*, *H*, *F*, and *G*. by using the function

$$\begin{aligned} &n_{12}\log(vD) - y_1 vD + n_{21}\log(\lambda) - y_2\lambda \\ &\quad + (n_{31}+n_{42})\log\varphi - (y_3+y_4)\varphi \\ &\quad + n_{13}\log(p\mu) - y_1 p\mu + n_{24}\log(q\mu) - y_2 q\mu, \end{aligned} \tag{1}$$

where p and q are correction factors needed in order to arrive at transition rates under the assumption of average behaviour of the other predators in the system ("Appendix: point 3"). The maximum likelihood estimators (and standard errors) are now

$$\hat{v} = \frac{n_{12}}{y_1 D} \pm \frac{\hat{v}}{\sqrt{n_{12}}}, \quad (2)$$

(i.e. the reciprocal of the average searching time times prey density per captured prey),

$$\hat{\lambda} = \frac{n_{21}}{y_2} \pm \frac{\hat{\lambda}}{\sqrt{n_{21}}}, \quad (3)$$

(i.e. the reciprocal of the average handling time per captured prey),

$$\hat{\varphi} = \frac{n_{31} + n_{42}}{y_3 + y_4} \pm \frac{\hat{\varphi}}{\sqrt{n_{31} + n_{42}}}, \quad (4)$$

(i.e. the reciprocal of the average fighting time), and (approximately)

$$\hat{\mu} = \frac{n_{13} + n_{24}}{p y_1 + q y_2} \pm \frac{\hat{\mu}}{\sqrt{n_{13} + n_{24}}}. \quad (5)$$

All four parameters v, μ, λ, and φ, were first estimated for each trial separately.

Assessing changes in v, μ, λ, and φ with changes in prey and competitor density

We subsequently distinguished five alternative models to estimate the parameters v, μ, λ, and φ. In the models, the parameters are estimated (1) using all data; this model is referred to as the constant-parameters model, (2) separately for each competitor density, (3) separately for each prey density, (4) separately for each combination of prey and competitor density, and (5) separately for each trial. We estimated v, μ, λ, and φ for each model using the procedure described previously and calculated the negative log-likelihood of that model using Eq. 1. Then we compared models using the likelihood ratio test to assess how parameter values varied with prey density, competitor density, and trial of each experiment.

Illustrating the strength of interference

Using the parameter estimates from the simplest model, the constant-parameters-model, we calculated the per capita feeding rate, W, of a predator using the stochastic version of the Beddington–DeAngelis model (Van der Meer and Smallegange 2009):

$$W(k) = \frac{vD}{Q(k)/Q(k-1)}, \quad (6)$$

where k is the number of predators in the system and the function $Q(k)$ is the sum of the relative limiting probabilities (limiting probabilities relative to the all-predators-are-searching state), and equals for $k = 1$–4:

$$\begin{aligned} Q(k) =& (1+\alpha)^k \\ &+ (k \geq 2)\binom{k}{2}\beta(1+2\alpha)(1+\alpha)^{k-2} \\ &+ (k \geq 4)\frac{\binom{k}{2}\binom{k-2}{2}}{2}\beta^2(1+2\alpha)^2(1+\alpha)^{k-4}, \end{aligned} \quad (7)$$

where $\alpha \equiv vD/\lambda$ and $\beta \equiv \mu/\varphi$. This equation can be expanded for a higher number of predators (Van der Meer and Smallegange 2009). We compared the predicted feeding rates with those observed for shore crabs. The strength of interference is then the reduction in per capita feeding rate when a predator forages with three rather than with one competitor.

Testing the equilibrium assumption

The use of limiting probabilities to derive the correction factors p and q in the log-likelihood function ("Appendix: point 3") assumes an equilibrium situation. In the experimental trials, after crabs were introduced in the experimental tank, all crabs started searching. As the start-up period (an arbitrarily chosen period prior to the experimental observations) progressed, encounters with prey and other crabs reduced the proportion of searching crabs and increased the proportion of crabs engaged in other behaviours. The question is, however, if the start-up period of the experimental trials was long enough for the predation process to reach or at least approach equilibrium. To test this, we simulated the time-series of the Markov chains for two and four predators and mimicked the experimental procedures to obtain 'observations' of y_1, y_2 and $y_3 + y_4$ expressed per prey capture ("Appendix: point 4"). We obtained these 'observations' for each predator–prey combination from 2,000 stochastic runs and used estimates of v, μ, λ, and φ from the constant-parameters-model. This model is the most conservative one as it assumes that v, μ, λ, and φ. are independent of prey and predator density. From Eqs. 2 and 3, it follows that the expected y_1 equals $n_{12}/(vD)$ and the expected y_2 equals n_{21}/λ. Expressed per prey capture $n_{12} = n_{21} = 1$ for the first experiment, and for the second experiment $n_{12} = n_{21} = 2$. The expected time that an individual spends fighting, i.e. interfering, while capturing one prey item ($y_3 + y_4$) follows a more complicated procedure. From the relative limiting probabilities, we first express the proportion of time an individual interferes per unit handling time. Multiplying this with the (constant) estimated handling time ($1/\lambda$) results in the expected absolute time that a predator interferes while capturing one prey item ("Appendix: point 5"). For a predator foraging with one competitor this equals:

$$E[y_3 + y_4] = \frac{1}{\lambda}\frac{\beta(1+2\alpha)}{(1+\alpha)\alpha},$$

with α and β as before: $\alpha = vD/\lambda$ and $\beta = \mu/\varphi$. For a predator foraging with three competitors, this equals:

$$E[y_3 + y_4] = \frac{1}{\lambda}\frac{3(1+2\alpha)\beta(1+\beta+\alpha(2+\alpha+2\beta))}{\alpha(1+\alpha)(1+3\beta+\alpha(2+\alpha+6\beta))}.$$

The three expected times, y_1, y_2, $y_3 + y_4$ (as a function of v, μ, λ, and φ estimated from the constant-parameters-model) can be compared to the simulated times. Both the simulated and the expected times are random (and exponentially distributed) variables and we compared the simulated times to the 95% confidence intervals of the expected times to assess if the start-up period was long enough for the predation process to reach equilibrium.

Results

The first step in assessing whether the stochastic version of the Beddington–DeAngelis model adequately describes foraging behaviour was to estimate the four parameters λ (1/handling time), φ (1/duration of an agonistic interaction), v (searching efficiency), and μ (rate of predator discovery) for each trial of each experiment. However, inspecting the resulting log-likelihoods showed that they were larger than expected in the first experiment (Table 1) and such results either suggest that the data from the first experiment were not exponentially distributed but were overdispersed, or that the data harbour outliers. Probability plots for the observed search, handling and interference times did not disprove the assumption on exponential distributions, underlying Markov models (Fig. 2). Yet, plotting the deviance residuals squared for each trial (where the deviance of model i is 2[log-likelihood full model—log-likelihood model i] divided by the difference in the number of parameters that are estimated in the full model and model i) revealed five outliers in the first experiment (Fig. 3). One outlier was due to kleptoparasitism as a result of which the search time of that focal crab was very long. The other four outliers were focal crabs that—for unknown reasons—needed much more search time than other focals (4 and 5 times more) or hardly any time (a tenth of the time the other focals needed) to find a prey item at low prey densities. After removal of these outliers, the apparent overdispersion vanished (Table 1). Estimates of the four parameters are shown for each experiment in Table 2.

Table 1 Results of the estimation procedures

Model	*df*	Original data		Outliers removed		Model versus	Δ *df*	χ^2	LL ratio
		LL	ϕ	LL	ϕ				
First experiment									
1.	2	−2,226.3	2.2	−1,664.1	1.4	–	–	–	–
2.	4	−2,216.0	2.0	−1,660.7	1.4	2 vs. 1	2	5.99	**6.8**
3.	8	−2,215.1	2.1	−1,657.3	1.3	3 vs. 1	6	12.59	**13.6**
4.	16	−2,203.6	2.0	−1,653.3	1.4	4 vs. 1	14	23.69	21.6
						4 vs. 2	12	21.03	14.8
						4 vs. 3	8	15.51	8.0
5.	80	−2,139.1	–	−1,609.1	–	5 vs. 2	76	97.35	**103.2**
						5 vs. 3	72	92.81	**96.4**
						5 vs. 4	64	83.68	**88.4**
Second experiment									
1.	2	−2,582.6	1.4			–	–	–	–
2.	4	−2,577.8	1.3			2 vs. 1	2	5.99	**9.6**
3.	6	−2,572.7	1.2			3 vs. 1	4	9.49	**19.8**
4.	12	−2,567.5	1.2			4 vs. 1	10	18.31	**30.2**
						4 vs. 2	8	15.51	**20.6**
						4 vs. 3	6	12.59	10.4
5.	96	−2,517.7	–			5 vs. 2	92	115.39	**120.2**
						5 vs. 3	90	113.15	110.0
						5 vs. 4	84	106.40	99.6

Dispersion parameters (ϕ) showed that, after removal of the five outliers (Fig. 3), the models of the first experiment were no longer overdispersed. The models of the second experiment were not overdispersed. For the model selection, we compared the log likelihood (LL) of nested models using the likelihood ratio test (LL ratio). In bold are models that provided a better fit against the simpler model at $\alpha = 0.05$

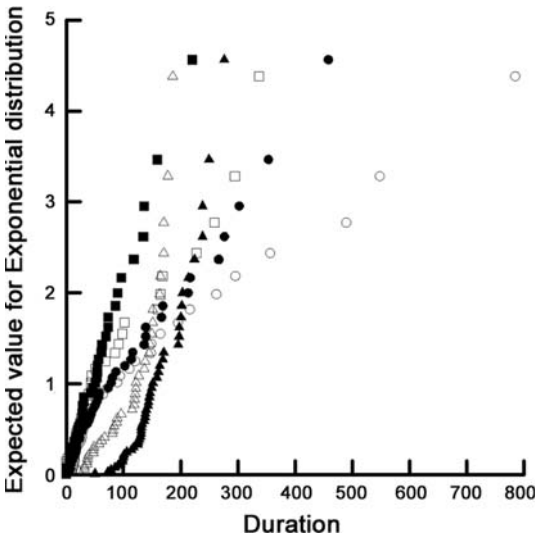

Fig. 2 Probability plots of the observed search times (*circles*), handling times (*triangles*) and interference times (*squares*) for the first experiment (*open symbols*) and the second experiment (*solid symbols*). The duration of these times is given in seconds. The plots should resemble a straight line if their distribution follows the exponential distribution

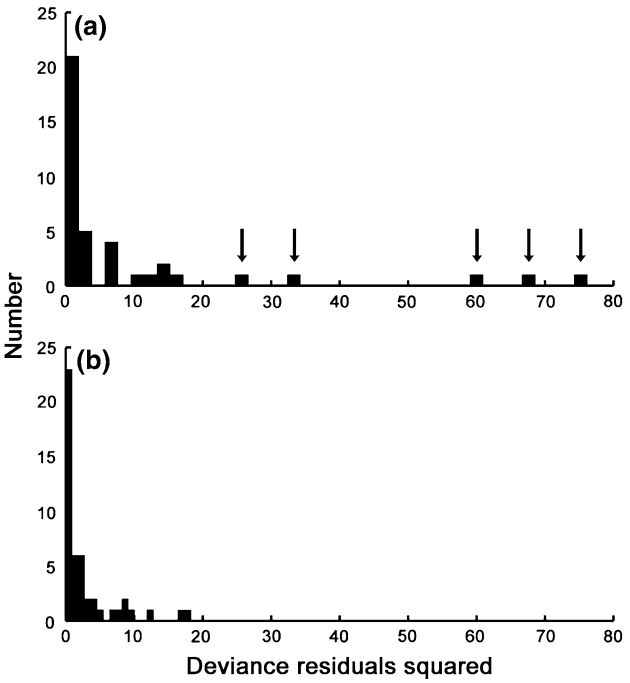

Fig. 3 Histograms of the deviance residuals squared of model 1 versus the full model 5. The *top panel* refers to the first experiment and shows the five outliers (denoted by *arrows*) (**a**) and the *bottom panel* refers to the second experiment (**b**)

The second step involved the model selection procedure to assess if the parameter values changed with changes in crab and prey density. For the first experiment, models 2 and 3 provided a better fit than model 1, and model 5 provided a better fit than models 2 and 3, suggesting that parameter values varied greatly between individual trials (Table 1). For the second experiment, model 4 gave a better fit than models 1 and 2 (Table 1). Model 5 did not provide a better fit than model 4 (Table 1), from which we infer that model 4 best described the data. This implies that parameter values varied with changes in crab and prey density in an interactive way. Plotting for experiment 1 the parameter estimates for models 2 and 3 (plotting the results according to model 5 would create a non-insightful cloud of observations), and for experiment 2 the parameter estimates for model 4 showed that the reciprocal of the handling time, λ, was constant over all prey densities and crab densities, except for a relatively high value at the highest prey density in the first experiment (Fig. 4). The reciprocal of the duration of an agonistic interaction was in the first experiment constant except for a high value at prey density 8 (Fig. 4). In the second experiment, this parameter was constant over all prey densities but tended to be higher at the higher crab density (Fig. 4). The searching rates for prey and predator showed more variation with changes in crab and prey density than λ and φ. Searching efficiency decreased with increasing crab density in the first experiment (Fig. 4). With increasing prey density, the lowest

Table 2 Estimates of λ (1/handling time), φ (1/duration of an agonistic interaction), v (searching efficiency), and μ (rate of predator discovery) for shore crabs foraging on mussels

P	*D*	λ		φ		v		μ	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
First experiment									
2	4	0.0099	0.0049	0.0890	0.0223	6.56	3.30	74.34	18.59
2	8	0.0087	0.0050	0.1160	0.0474	3.10	1.79	33.96	13.87
2	16	0.0112	0.0050	0.0930	0.0351	3.22	1.44	46.49	17.57
2	32	0.0176	0.0079	0.0948	0.0547	4.73	2.12	56.02	32.34
4	4	0.0086	0.0043	0.0794	0.0136	4.16	2.08	47.60	8.16
4	8	0.0101	0.0045	0.1246	0.0171	1.38	0.62	38.71	5.32
4	16	0.0065	0.0033	0.0643	0.0117	1.53	0.77	49.89	9.11
4	32	0.0119	0.0053	0.0911	0.0275	2.61	1.17	42.64	12.86
Overall		0.0101	0.0017	0.0899	0.0005	2.63	0.45	42.47	0.26
Second experiment									
2	8	0.0072	0.0025	0.1164	0.0198	2.15	0.76	52.28	8.90
2	32	0.0073	0.0026	0.0872	0.0203	1.20	0.42	58.45	13.59
2	128	0.0087	0.0031	0.0918	0.0325	1.40	0.50	97.36	34.42
4	8	0.0055	0.0019	0.1322	0.0129	1.72	0.61	51.35	5.00
4	32	0.0058	0.0021	0.1246	0.0154	0.95	0.34	59.62	7.37
4	128	0.0068	0.0024	0.1220	0.0219	0.51	0.18	53.91	9.68
Overall		0.0067	0.0001	0.1210	0.0005	1.07	0.16	51.43	0.20

Parameters were estimated separately for each trial and are summarized by predator density (*P*) and prey density (*D*). Estimates for the first experiment were obtained after removal of five outliers (Fig. 3). λ and φ are in 1/s, and the rates in cm^2 per s

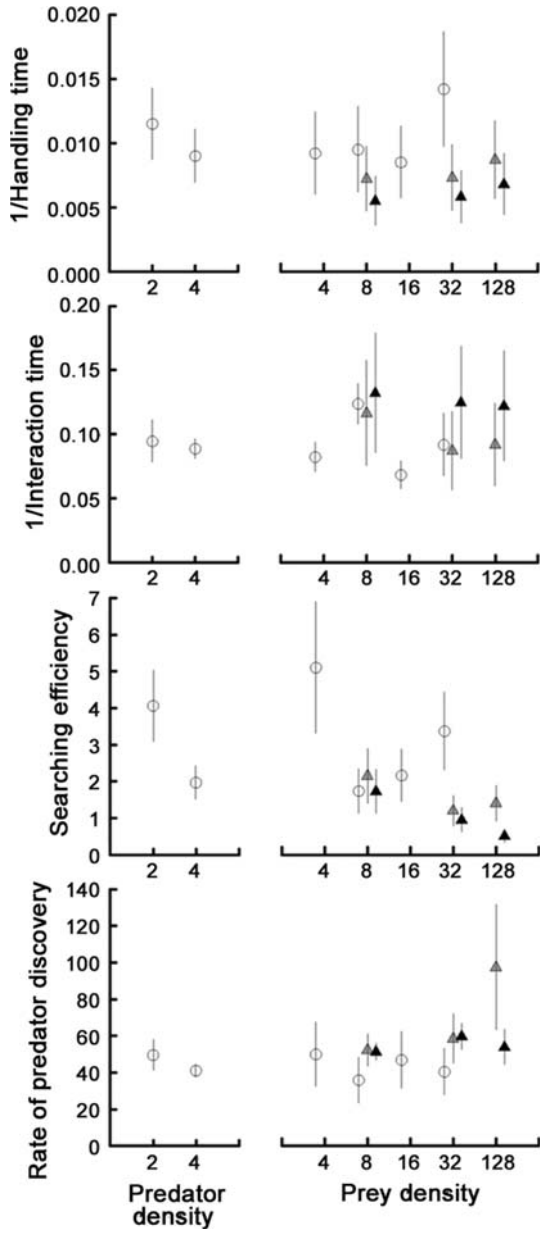

Fig. 4 The four parameters 1/handling time (λ), 1/duration of an agonistic interaction (φ), searching efficiency (v) and rate of predator discovery (μ) (±SE) for experiment 1 (*circles*) and experiment 2 (*grey triangles*: two crabs; *black triangles*: four crabs). Both rates are in cm^2 per s and λ and φ are in 1/s

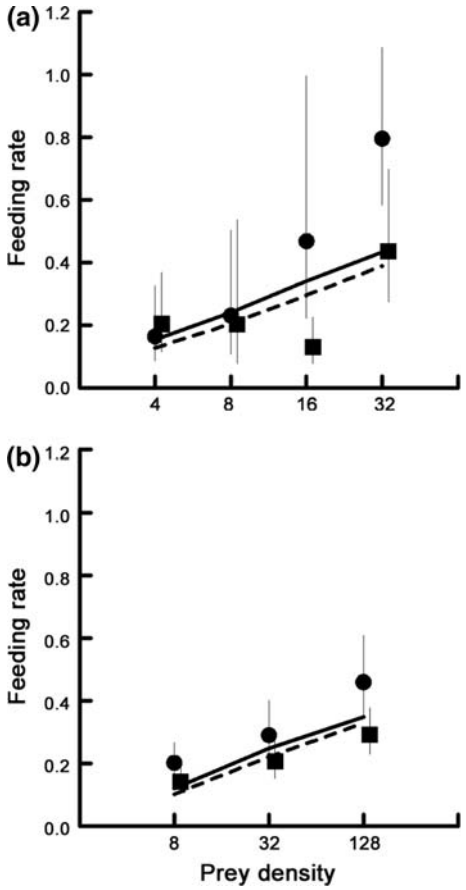

Fig. 5 Illustrating the strength of interference using the data of the first (**a**) and second (**b**) experiment. The *lines* are the predicted feeding rates (Eq. 6) (no. per min) of a crab foraging with one competitor (*solid lines*) and with three competitors (*dashed lines*). The following parameter values were used (estimated using the simplest model): handling time ($1/\lambda$) was 99.0 s (experiment 1) and 149.3 s (experiment 2); the average duration of an agonistic encounter ($1/\varphi$) was 11.1 s (experiment 1) and 8.3 s (experiment 2); searching efficiency (v) was 2.6 cm^2 per s (experiment 1) and 1.1 cm^2 per s (experiment 2); rate of predator discovery (μ) was 42.5 cm^2 per s (experiment 1) and 51.4 cm^2 per s (experiment 2). The *symbols* show the observed feeding rates (no. per min ±95% CI) of shore crabs foraging with one competitor (*circles*) and with three competitors (*squares*). Prey densities are in no. per ¼ m^2

value was at intermediate prey densities, whereas in the second experiment, searching efficiency was lowest at the highest prey and crab density (Fig. 4). Rate of predator discovery was constant for both crab densities in the first experiment. With increasing prey density, in the second experiment, rate of predator discovery tended to increase with increasing prey density at the lowest crab density (Fig. 4). At the highest crab density, rate of predator discovery was constant over all prey densities (Fig. 4).

The third step involved implementation of the parameter values estimated from the constant-parameters-model in the stochastic version of the Beddington–DeAngelis model to calculate per capita feeding rates as a function of prey and predator density. These expected feeding rates appeared to match those observed in the experiments, except for two predator–prey combinations of the first experiment, '2–32' and '4–16', where the 95% confidence intervals of the observed feeding rates did not overlap with the expected feeding rates (Fig. 5).

The parameter estimation procedure for the behaviour of a focal predator is based on the assumption that the states of its competitors are in equilibrium. To test this

assumption, we simulated each experiment (again using the parameter estimates of the constant-parameters-model) and compared the simulated and expected y_1, y_2 and $y_3 + y_4$ expressed per mussel capture. Simulated times did not deviate from the expected times, from which we infer that the start-up period was long enough for the predation process to approach an equilibrium (Table 3).

Discussion

We assessed how adequate the stochastic version of the Beddington–DeAngelis functional response model is in describing foraging behaviour and interference in a small predator population. Probability plots for the observed search, handling and interference times revealed that the assumption on exponential distributions, which underlie Markov chains, was justified. In many behavioural experiments, the foraging behaviour of only a few predators is investigated, which contrasts with deterministic interference models that assume that the predator population is large enough to be treated as a continuous variable. The stochastic version of the Beddington–DeAngelis functional response model overcomes this problem and is also not constrained by the assumption of weak interference, as were previous deterministic models of the generalized functional response (Moody and Houston 1995; Ruxton et al. 1992; Ruxton and Moody 1997).

We estimated the four parameters of the model from behavioural data on shore crabs foraging on mussels and assessed if their values changed with changes in prey or predator density. The reciprocal of the handling time of a prey item (λ) and the reciprocal of the duration of an agonistic interaction (φ) both showed little variation with changes in prey or predator density. The searching rates for prey and competitors showed pronounced changes with prey or predator density. In the first experiment, the searching efficiency of crabs decreased with increasing predator density. Perhaps crabs were more vigilant towards each other at the highest crab density. Vigilance in crabs is difficult to separate from their actual searching behaviour in behavioural observations (Smallegange and Van der Meer 2007), in which case an increase in vigilance would lead to an increase in search time per prey capture and hence to an apparent decrease in searching efficiency. Similarly, in the second experiment, this might have been the reason why searching efficiency was lowest at the highest crab density when prey was most abundant. The rate of predator discovery varied little with changes in prey and predator density although in the second experiment it tended to increase with increasing prey density.

Estimates of the parameters of a functional response model are usually obtained by fitting observed feeding rates against those predicted by the model (Abrams 1990). Even when the fit between observed and predicted feeding rates is adequate, the actual values of the functional response parameters seldom match those determined from direct behavioural observations (Abrams 1990, Taylor and Collie 2003). The maximum likelihood estimators of λ and φ are, however, equivalent to how one would determine parameter values from behavioural observations. The searching rates for prey and competitor, ν and μ, are more difficult to determine from behavioural observations, yet maximum likelihood estimators, and the new estimation procedure presented here using correction factors, are an obvious starting point. Unfortunately, we cannot assess the accuracy of our estimates of ν and μ because, to our best knowledge, actual measurements of searching efficiency and rate of predator discovery of shore crabs have not been published before. We expect, however, that the searching efficiency of crabs that forage for buried bivalve prey is low. Crabs search for buried prey by probing the sand with their walking legs (Crothers 1968), which causes them to cover only a small area searched per unit of time. Because searching efficiency is related to the walking or searching speed of crabs, a numerical exercise can be performed to assess the accuracy of the parameter estimates. For example, in the presence of cracked bivalve prey, the walking speed of blue crabs (*Callinectes sapidus*) was 10 cm per s, and in the absence of prey 8 cm per s (Finelli et al. 2000). Shore crabs are smaller than blue crabs and their walking speed is most likely lower than 10 cm per s. Suppose crabs walk 5 cm per s in one direction. From the-constant-parameter-model, the searching efficiency of shore crabs was estimated between 1.1 and 2.6 cm^2 per s; the width of the (rectangular) search area covered per second is then between 0.2 and 0.5 cm. A similar exercise can be done for the rate of predator discovery. Because crabs have good vision (Warner 1977), we expect that the rate with which they encounter competitors is much higher than the rate with which they find prey. From the constant-parameters-model, the rate of predator discovery was estimated between 43 and 51 cm^2 per s. If, again, crabs would walk 5 cm per s, then the width of the (rectangular) area within which they 'attack' conspecifics is between 8.6 and 10.2 cm. Because neither searching efficiency, nor rate of predator discovery and attack distance has been measured before, the above indirect estimates cannot be tested against direct observations.

Although the values of some foraging parameters changed with changes in prey and predator density, incorporating constant parameter values in the stochastic Beddington–DeAngelis model showed a good fit between observed and expected feeding rates, and hence a good prediction of the strength of interference in shore crabs. For two predator–prey combinations, the prediction deviated

Table 3 Can we assume that each experiment was in equilibrium?

Prey	Expected times based on ML estimators and relative limiting probabilities			Average of the simulated times		
	y_1	y_2	$y_3 + y_4$	y_1	y_2	$y_3 + y_4$
Two crabs						
4	237.6	99.2	57.1	236.6	99.3	57.1
(E1)	(6.0–876.6)	(2.5–365.9)	(1.5–214.0)			
8	118.8	99.2	32.7	122.8	95.0	32.7
(E1)	(3.0–438.3)	(2.5–365.9)	(0.8–120.3)			
8	292.1	148.6	49.2	295.8	148.4	47.6
(E2)	(7.4–1,077.4)	(3.8–548.2)	(1.2–181.4)			
16	59.4	99.2	18.2	60.8	99.4	18.0
(E1)	(1.5–219.2)	(2.5–365.9)	(0.5–67.2)			
32	29.7	99.2	9.9	29.5	99.8	10.3
(E1)	(0.8–109.6)	(2.5–365.9)	(0.3–36.6)			
32	73.0	148.6	15.4	72.4	149.7	19.6
(E2)	(1.8–269.3)	(3.8–548.2)	(0.4–56.6)			
128	18.3	148.6	4.3	18.8	148.4	5.6
(E2)	(0.5–67.3)	(3.8–548.2)	(0.1–16.0)			
Four crabs						
4	237.6	99.2	134.5	232.6	96.2	132.4
(E1)	(6.0–876.6)	(2.5–365.9)	(3.4–496.2)			
8	118.8	99.2	77.6	122.5	97.3	77.1
(E1)	(3.0–438.3)	(2.5–365.9)	(3.4–286.3)			
8	292.1	148.6	158.4	295.3	149.9	150.5
(E2)	(7.4–1,077.4)	(3.8–548.2)	(4.0–584.4)			
16	59.4	99.2	45.3	60.6	100.7	45.2
(E1)	(1.5–219.2)	(2.5–365.9)	(1.1–167.1)			
32	29.7	99.2	26.0	29.7	99.5	26.1
(E1)	(0.8–109.6)	(2.5–365.9)	(0.7–96.0)			
32	73.0	148.6	53.3	71.6	149.4	50.5
(E2)	(1.8–269.3)	(3.8–548.2)	(1.3–196.7)			
128	18.3	148.6	16.5	18.7	147.4	15.6
(E2)	(0.5–67.3)	(3.8–548.2)	(0.4–61.0)			

Shown are the expected y_1, y_2 and $y_3 + y_4$ expressed per prey capture calculated from the maximum likelihood (ML) estimators and relative limiting probabilities. We ran 2,000 stochastic runs to simulate each experiment (denoted as E1 and E2) using the values of ν, μ, λ, and φ estimated according to the simplest model. We compared the average of the simulated times with the 95% confidence intervals of the expected times to assess if the acclimation period of the experiments was long enough to reach equilibrium. Confidence intervals are given in brackets. None of the simulated times differed from the expected times. Prey and predator densities are in no. per ¼ m^2. Times are in seconds

from the observation. In the first case, the observed feeding rate was higher than predicted (Fig. 5). In the second case, it was lower than predicted (Fig. 5), most likely because, unlike in other predator–prey combinations prey were stolen from the focal crabs on a number of occasions. This increased the search time required to find a prey item, which lowered the feeding rate (Smallegange et al. 2006). Kleptoparasitism is a phenomenon that was not incorporated in the Markov chains of our model. Based on earlier work (Ruxton and Moody 1997; Broom and Ruxton 1998), Yates and Broom (2007) developed a stochastic interference model that includes kleptoparasitism and found that the original deterministic models approximated the stochastic model well in most situations. This matches our recent finding that, in the absence of kleptoparasitism, the stochastic version of the Beddington–DeAngelis model matches the deterministic version for a larger number of predators (more than five or six) (Van der Meer and Smallegange 2009). Future studies should reveal if this conclusion holds if kleptoparasitism is introduced into the stochastic version of the Beddington–DeAngelis model.

Assuming constant parameter values, interference in our model occurs through time lost in agonistic interactions: as the number of competitors increases, the chance of

encountering a competitor increases and more time is spent in aggressive interactions. This mechanism of interference is observed in several predator–prey systems (Cresswell 1998; Smallegange et al. 2006; Smallegange and Van der Meer 2007; Vahl et al. 2005) and is central to theoretical studies that model interference from basic foraging behaviour using ordinary differential equations (Holmgren 1995; Moody and Houston 1995; Ruxton et al. 1992) or Markov chains (Van der Meer and Smallegange 2009). Although the strong match between observed feeding rates of shore crabs and those predicted using the constant-parameters-model is gratifying, our model is still a simplification of reality. The next step is to incorporate the digestion of prey (Jeschke et al. 2002) and to assess how adequate the stochastic version of the Beddington–DeAngelis functional response model is in predicting the distribution of predators (Holmgren 1995; Moody and Houston 1995).

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Appendix: Markov chains of the foraging process

1. States and transition rates

The transition matrix of the focal-predator Markov chain of one predator consists of the behavioural states *S* and *H* with associated transition rates vD and λ (Table 4). The states and transition rates in the transition matrix of the two and three predator Markov chain are shown in such a way that the behaviour of the focal predator and that of the other predators is easily interpreted (Tables 4, 5): the four states are lumped according to the state of the focal predator: (*S*) focal predator is searching, (*H*) focal predator is handling, (*F*) focal predator is fighting after searching, and (*G*) focal predator is fighting after handling.

2. Limiting probabilities

The probability that a continuous-time Markov chain will be in state j at time t converges under certain conditions to a limiting value, or limiting probability, independent of the initial state (Ross 1989, pp. 268–275). These conditions hold for models of the kind considered here. The limiting probability of each state is then the time that the Markov chain, or the foraging process of the predators, is in that state. For each Markov chain, the limiting probabilities were derived relative to the limiting probability for the 'all searching' state. They are referred to as relative limiting probabilities and are given in Tables 4 and 5.

Table 4 Transition matrix of the 1-predator and 2-predator Markov chain

One predator				Two predators									
						S	**S**	**H**	**H**	**F**	**F**	**G**	
	S	**H**	rlp			S	H	S	H	F	G	F	rlp
S	-	$\boldsymbol{vD}$	1	**S**	S	-	vD	$\boldsymbol{vD}$	0	$\boldsymbol{\mu}$	0	0	1
H	$\boldsymbol{\lambda}$	-	α	**S**	H	λ	-	0	$\boldsymbol{vD}$	0	$\boldsymbol{\mu}$	0	α
				H	S	$\boldsymbol{\lambda}$	0	-	vD	0	0	$\boldsymbol{\mu}$	α
				H	H	0	$\boldsymbol{\lambda}$	λ	-	0	0	0	α^2
				F	F	$\boldsymbol{\varphi}$	0	0	0	-	0	0	β
				F	G	0	$\boldsymbol{\varphi}$	0	0	0	-	0	$\alpha\beta$
				G	F	0	0	$\boldsymbol{\varphi}$	0	0	0	-	$\alpha\beta$

The 2-predator Markov chain shows the behaviour of the focal predator in bold, and that of the other predator in non-bold letters. The states denote searching (S), handling (H), fighting after searching (F), and fighting after handling (G), v is the searching efficiency, D the density of prey, μ the rate of predator discovery, λ the handling time and φ the duration of an interaction. For an explanation of α and β, see main text. 'rlp' is the relative limiting probability of each state, i.e. its limiting probability relative to the limiting probability for the 'all searching' state (S, respectively SS). Light grey areas denote transitions from searching to handling and visa versa. Intermediate grey areas denote transitions into a fighting state, and the dark grey areas denote transitions from fighting back to searching or handling. White areas denote no transitions between states. Transitions where the state of the focal predator changes are given in bold; transitions where the state of the focal predator does not change are given in non-bold letters

3. Rationale behind maximum likelihood estimators when only the focal predator is observed

From the Markov chains for two and three predators, it appears that the transitions from *S* to *H* (rate vD), from *H* to *S* (rate λ), from *F* to *S* (rate φ) and from *G* to *S* (rate φ) have a constant transition rate, independent of the behaviour of the other predators. The only problem concerns the transitions from *S* to *F* and from *H* to *G*, which do depend upon the states of the other(s). To cope with this problem, we have assumed that the states of the others are in equilibrium and are thus proportional to the limiting probabilities. Using this approximation (where necessary), the maximum likelihood approach, as described by Van der Meer and Smallegange (2009) can be used to estimate the parameters v, μ, λ, and φ, and their maximum likelihood estimators are given in the main text. In the log-likelihood function, the correction factors p and q were introduced, because, if only the behaviour of a focal predator is observed, they are needed in order to arrive at transition rates under the assumption of average behaviour of the other predators in the system. Table 6 can be used to derive the correction factors p and q. For two predators, the state of the non-focal predator does not matter for the transition from the focal predator state *S* to the focal-predator state *F*.

Table 5 Transition matrix of the foraging process of three predators, showing the behaviour of the focal predator (in bold) and the other predators (non-bold letters)

		S SS	**S** HS	**S** HH	**S** FF	**S** FG	**H** SS	**H** HS	**H** HH	**H** FF	**H** FG	**F** FS	**F** FH	**F** GS	**F** GH	**G** FS	**G** FH	
		SS	HS	HH	FF	FG	SS	HS	HH	FF	FG	FS	FH	GS	GH	FS	FH	rlp
S	SS	–	$2\nu D$	0	μ	0	$\boldsymbol{\nu D}$	0	0	0	0	$\boldsymbol{2\mu}$	0	0	0	0	0	1
S	HS	λ	–	νD	0	μ	0	$\boldsymbol{\nu D}$	0	0	0	0	$\boldsymbol{\mu}$	$\boldsymbol{\mu}$	0	0	0	2α
S	HH	0	2λ	–	0	0	0	0	$\boldsymbol{\nu D}$	0	0	0	0	0	$\boldsymbol{2\mu}$	0	0	α^2
S	FF	φ	0	0	–	0	0	0	0	$\boldsymbol{\nu D}$	0	0	0	0	0	0	0	β
S	FG	0	φ	0	0	–	0	0	0	0	$\boldsymbol{\nu D}$	0	0	0	0	0	0	$2\alpha\beta$
H	SS	$\boldsymbol{\lambda}$	0	0	0	0	–	$2\nu D$	0	μ	0	0	0	0	0	$\boldsymbol{2\mu}$	0	α
H	HS	0	$\boldsymbol{\lambda}$	0	0	0	λ	–	νD	0	μ	0	0	0	0	0	$\boldsymbol{\mu}$	$2\alpha^2$
H	HH	0	0	$\boldsymbol{\lambda}$	0	0	0	2λ	–	0	0	0	0	0	0	0	0	α^3
H	FF	0	0	0	$\boldsymbol{\lambda}$	0	φ	0	0	–	0	0	0	0	0	0	0	$\alpha\beta$
H	FG	0	0	0	0	$\boldsymbol{\lambda}$	0	φ	0	0	–	0	0	0	0	0	0	$2\alpha\beta^2$
F	FS	$\boldsymbol{\varphi}$	0	0	0	0	0	0	0	0	0	–	νD	0	0	0	0	2β
F	FH	0	$\boldsymbol{\varphi}$	0	0	0	0	0	0	0	0	λ	–	0	0	0	0	$2\alpha\beta$
F	GS	0	$\boldsymbol{\varphi}$	0	0	0	0	0	0	0	0	0	0	–	νD	0	0	$2\alpha\beta$
F	GH	0	0	$\boldsymbol{\varphi}$	0	0	0	0	0	0	0	0	0	λ	–	0	0	$2\alpha^2\beta$
G	FS	0	0	0	0	0	$\boldsymbol{\varphi}$	0	0	0	0	0	0	0	0	–	νD	$2\alpha\beta$
G	FH	0	0	0	0	0	0	$\boldsymbol{\varphi}$	0	0	0	0	0	0	0	λ	–	$2\alpha^2\beta$

See for explanation of symbols and colouration Table 4. Transitions where the state of the focal predator changes are given in bold; transitions where the state of the focal predator does not change are given in non-bold letters

Whatever the other is doing (searching or handling), the two predators will start a fight when they encounter each other (which happens with a rate equal to μ). The factor p therefore equals 1 (Table 6). When the focal predator is handling the ratio of the time that the other predator is searching equals $1/(1+\alpha)$, where α is $\nu D/\lambda$. Only in that case, will the two predators start a fight. Hence, q equals $1/(1+\alpha)$. Similarly, it can be derived from Table 6 (summing the products of the number of possible fights times the relative limiting probability and dividing that sum by the sum of the relative limiting probabilities) that for three predators

$$p = \frac{2(1+\alpha)^2}{(1+\alpha)^2+\beta(1+2\alpha)} \quad \text{and } q = \frac{2(1+\alpha)}{(1+\alpha)^2+\beta(1+2\alpha)},$$

and for four predators

$$p = \frac{3(1+\alpha)^3+3\beta(1+5\alpha)}{(1+\alpha)^3+3\beta(1+5\alpha)} \quad \text{and}$$

$$q = \frac{3(1+\alpha)^2+3\beta(1+2\alpha)}{(1+\alpha)^3+3\beta(1+5\alpha)}.$$

These correction factors require knowledge of α and of $\beta = \mu/\varphi$, and thus of μ itself. Henceforth, an iterative procedure has to be used to estimate μ. Starting with a guestimate of μ, and thus of p and q, an estimate of the parameter μ is obtained by using Eq. 5. This estimate is then used to obtain new values for p and q, which in turn are used for a new estimate of μ. This procedure is repeated until convergence is obtained. Data from separate trials can be lumped in the parameter estimation procedure.

4. Simulating the foraging behaviour

For the focal-predator Markov chain of two predators six stochastic reactions—the transitions between states (cf. Table 4)—can be specified. For the focal-predator Markov chain of four predators, we specified the stochastic reactions of one individual of the predator population and lumped the stochastic reactions of the remainder of the predator population. The order and timing of the stochastic reactions proceeds as follows (Ross 1989). Each reaction has an associated rate, or hazard, and at a given point in time all hazards are calculated and summed to give the total event hazard R. The time to the next event is drawn from an exponential distribution with mean $1/R$. One out of all possible reactions is then selected to occur at the next time-point, and each reaction has a probability of being selected equal to its associated hazard divided by the total event hazard R. The simulation then proceeds to the next time-point. This procedure is repeated until a pre-defined final time or event is reached.

We simulated each experiment by mimicking the 'experimental procedure', of the two experiments in Smallegange et al. (2006). In the experiments, prior to each trial, crabs were allowed to acclimatize to the tank for an arbitrarily chosen time period of 10 min. In each trial, the foraging behaviour of one focal crab was scored. The first experiment was concerned with the time period in which

Table 6 Number of possible transitions (no. of fights) from the focal predator states S or H towards F/G, depending upon the states of the other predators in the system

Focal	Others	No. fights	rlp	Focal	Others	No. fights	rlp
Two predators				*Four predators*			
S	S	1	1	S	S3	3	1
S	H	1	α	S	S2H	3	3α
H	S	1	α	S	SH2	3	$3\alpha^2$
H	H	0	α^2	S	H3	3	α^3
				S	SF2	1	3β
Three predators				S	HF2	1	$3\alpha\beta$
S	S2	2	1	S	SG2	1	$6\alpha\beta$
S	H1S1	2	2α	S	HG2	1	$6\alpha\beta$
S	H2	2	α^2	H	S3	3	α
S	F2	0	β	H	S2H	2	$3\alpha^2$
S	F1G1	0	$2\alpha\beta$	H	SH2	1	$3\alpha^3$
H	S2	2	α	H	H3	0	α^4
H	H1S1	1	$2\alpha^2$	H	SF2	1	$3\alpha\beta$
H	H2	0	α^3	H	HF2	0	$3\alpha^2\beta$
H	F2	0	$\alpha\beta$	H	SG2	1	$6\alpha^2\beta$
H	F1G1	0	$2\alpha^2\beta$	H	HG2	0	$6\alpha^2\beta$

rlp is the relative limiting probability; for an explanation of α and β see main text. For 2, 3, and 4 predators, respectively. Numbers next to each state denote the number of individuals in that state

the focal crab searched for and ate a single mussel. The second experiment was concerned with two consecutive time periods in which the focal crab searched for and ate a mussel. In the simulations, all individuals started in the searching state. After a 'start-up period' of 10 min, the 'observation' started after the focal individual had consumed the first prey item. For comparison with the first experiment, the 'observation period' ended when the focal individual had consumed the second prey item, and for comparison with the second experiment, the 'observation period' ended when the focal individual had consumed the third prey item.

5. Calculating $y_3 + y_4$ from the relative limiting probabilities

The expected time that an individual spends fighting, i.e. interfering, while capturing one prey item ($y_3 + y_4$), is calculated using the relative limiting probabilities of the Markov chains. That is, from the relative limiting probabilities we first express the proportion of time an individual interferes per unit handling time by summing the relative limiting probabilities of the states in which the focal crab is in the behavioural state F or G, I^*, and dividing this over the sum of all relative limiting probabilities, P^*.

The proportion of time that a predator handles a prey item, H^*/P^*, is likewise derived, and dividing I^*/P^*over H^*/P^*gives the proportion of time an individual interferes per unit handling time. For a predator foraging with one competitor this equals:

$$\frac{\beta + 2\alpha\beta}{\alpha + \alpha^2},$$

and for a predator foraging with three competitors this equals:

$$\frac{3\beta^2 + 3\beta + 12\alpha\beta^2 + 12\alpha\beta + 12\alpha^2\beta^2 + 15\alpha^2\beta + 6\alpha^3\beta}{\beta + 3\alpha\beta + 3\alpha^2 + 9\alpha^2\beta + 3\alpha^3 + 6\alpha^3\beta + \alpha^4},$$

(relative limiting probabilities for the Markov chain of four predators can be found in Van der Meer and Smallegange 2009). Multiplying each equation with the (constant) estimated handling time for one prey item ($1/\lambda$) results in the expected absolute time that a predator interferes while capturing one prey item ($E[y_3 + y_4]$).

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